18. INVASIONS OF FOREST COMMUNITIES DURING THE HOLOCENE: BEECH AND HEMLOCK IN THE GREAT LAKES REGION

MARGARET BRYAN DAVIS
Department of Ecology and Behavioral Biology, University of Minnesota
Minneapolis, Minnesota 55455, USA

INTRODUCTION

During the Holocene (the last 10 000 years) boreal and temperate tree species advanced into deglaciated regions of North America at rates averaging 100–400 m per year (Davis 1981a.) Similar rates are documented in Europe (Firbas 1949; Huntley & Birks 1983).

How were such rapid rates of range extension possible? Many ecologists feel that seed dispersal and establishment must have limited the speed of range extension (Iverson 1954; Davis 1961, 1976; Walker 1982), while others consider climatic boundaries and their changes in space and time the most important factors (T. Webb 1986). Van der Pijl (1969, p. 22) reviewed mechanisms of seed dispersal, and concluded that the estimated rates of spread seem appropriate only for pioneer species, 'exceeding regular possibilities' for late-successional trees. Walker (1982) placed emphasis on establishment and competition by suggesting that periodic disturbances could have facilitated rapid range extension by opening forest communities to invasion. The fossil record in North America shows that pioneer species did attain the most rapid rates of range extension. Nevertheless, late-successional trees diffused onto a forested landscape at rates as rapid as 200 m per year. It is my purpose here to discuss the mechanisms by which shade-tolerant, long-lived and generally slow-growing late-successional tree species were able to extend their ranges rapidly and to invade forest communities.

History of beech and hemlock in the Great Lakes region

For the past several years we have been studying fossil pollen at a network of sites, in order to learn how beech (*Fagus grandifolia*) and hemlock (*Tsuga canadensis*) moved into the Great Lakes region (Davis *et al.* 1986; K.D. Woods & M.B. Davis, unpubl.; Webb 1982; M.W. Schwartz, unpubl.). Beech and hemlock were chosen for study because (i) they entered the region at about the same time, (ii) they commonly co-occur in northern hardwoods forests, and (iii) they both reach their western limits in this region. The original focus of the research was on seed dispersal. The Great Lakes are geographical barriers 100 km wide: if trees cannot disperse across barriers, the Great Lakes will cause delays in range extensions. The two tree species provided a useful comparison, because beech seeds are dispersed by animals, whereas hemlock seeds are dispersed by wind.

Beech and hemlock produce pollen that is readily identified in sediments. We have compared pollen deposited in sediments 150 years ago, before logging and forest clearance, with nineteenth century forest records from the federal Land Office Survey. There are quantitative relationships between the pollen percentages and tree abundances (Schwartz 1985). Beyond the species limits pollen percentages drop rapidly to background levels below 1%, assuring us that species limits can be recognized within 30–50 km from the quantities of pollen in lake sediments (M.B. Davis, M.W. Schwartz & K.D. Woods, unpubl.). The latter relationship means that fossil pollen can be used to map the species' frontiers as they advanced into the region.

A recent paper summarizing our results presents maps of pollen percentages of beech and hemlock at 1000-year intervals (Davis *et al.* 1986). We included data from twenty-one sites we have investigated, plus thirty published studies by other authors that extend the area of study (Fig. 18.1). Figure 18.2 summarizes our interpretation of the results, showing the inferred locations of the species frontiers at 1000-year intervals. Hemlock pollen first appeared at scattered sites in Upper and Lower Michigan. These scattered colonies apparently originated from seeds transported long-distance from Ontario, where hemlock was established about 8000 years BP (McAndrews, 1970, 1981; Kapp, 1977; Liu, 1982). Hemlock populations expanded rapidly and spread over a large region (>50 000 km^2) by 5000 years BP . Its subsequent spread to the west and south-west occurred much more slowly; it reached its present limit in Wisconsin about 1500 years ago (unpubl. data).

Beech invaded lower Michigan from the south, extending its range northward at a relatively rapid rate. Between 6000 and 5000 years BP , an outlying population was established across the lake in Wisconsin. Beech dispersed to Wisconsin either directly across the lake, or around its southern end, across what is presently a disjunction in the beech range. At that time the predominant vegetation in the area of the disjunction was prairie, but beech may have dispersed distances of 25–50 km between scattered patches of forest growing in ravines and other protected sites (Webb 1983). A second dispersal event occurred 4000 years BP, when

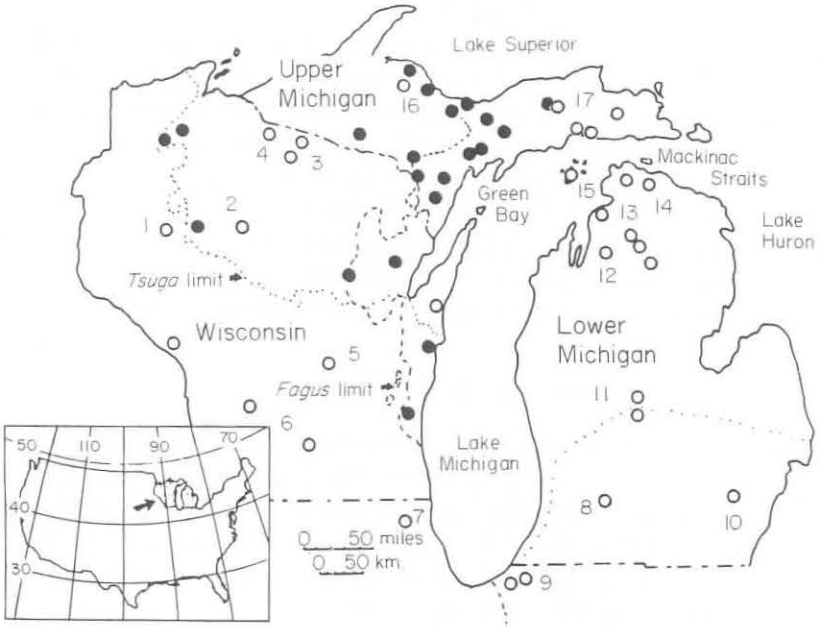

FIG. 18.1. Map of the northern Great Lakes region. Black dots indicate the locations of small lakes from which we have prepared pollen diagrams (Davis *et al.* 1986). Open circles indicate the locations of sites of pollen diagrams reported in the literature as follows: (1) Peters & Webb 1979; (2) Heide 1981; (3) Webb 1974; (4) Swain 1978; (5) Maher 1982; West 1961; (6) Davis 1977; (7) King 1981; (8) Manny, Wetzel & Bailey 1978; (9) Bailey 1972; (10) Kerfoot 1974; (11) Kapp 1977; Gilliam, Kapp & Bogue 1967; (12) Lawrenz 1975; (13) Bernabo 1981; (14) R.P. Futyma, unpublished; (15) Kapp *et al.* 1969; (16) Brubaker 1975; (17) Futyma 1982. (Figure modified from Davis *et al.* 1986.)

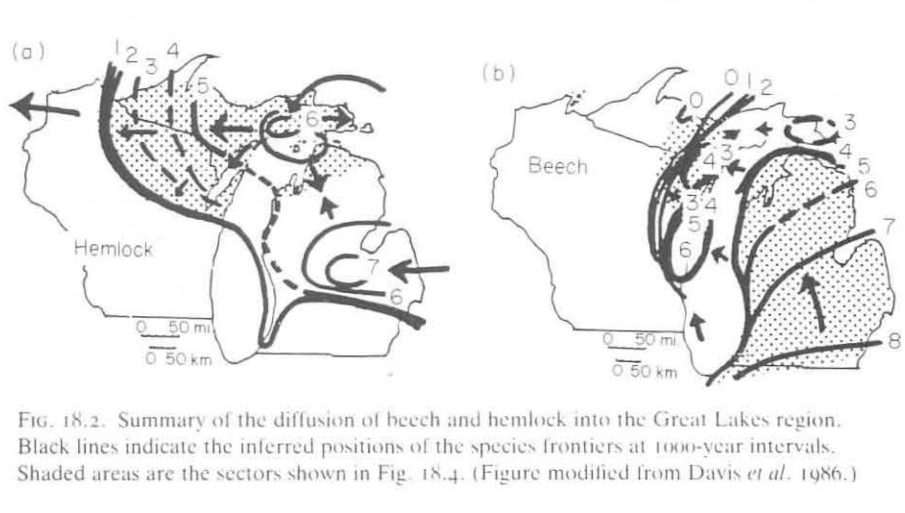

FIG. 18.2. Summary of the diffusion of beech and hemlock into the Great Lakes region. Black lines indicate the inferred positions of the species frontiers at 1000-year intervals. Shaded areas are the sectors shown in Fig. 18.4. (Figure modified from Davis *et al.* 1986.)

another outlying population became established on the west side of Green Bay in Upper Michigan. Rapid expansion of range occurred around 2500 years BP when beech colonized the eastern half of Upper Michigan. The range limit was fairly stable between 2000 and 500 years BP, but within the last several centuries an outlying population was established about 50 km to the west, and the limit of continuous populations advanced about 20 km (K.D. Woods & M.B. Davis, unpubl.).

The data are used in this chapter as the basis for a general discussion of factors that affect range extension and invasion of forest communities.

DIFFUSION MODELS

Parameters affecting the rate of advance of a species frontier are dispersal and population growth rate (Okubo 1980). These variables are the most important in attempting to explain the complex patterns of range expansion recorded by fossil pollen. The mode of seed dispersal is fixed for most species, but the probabilities of seed arriving at favourable sites vary, depending on seed production and on the availability and behaviour of biotic vectors and/or wind patterns. Population growth rates are also variable, depending on climate, soils, and the biotic environment.

To focus the discussion, I am considering two models of diffusion, a continuous front model (A), and a model where discontinuous populations are established far in advance of the front (B) (Fig. 18.3). In Model A, the rate of advance of the species frontier depends on the average distance of seed dispersal per generation and on the number of years per generation. The seed rain is assumed to decrease exponentially away from the source tree. Model B invokes occasional dispersal of seeds very great distances. No particular statistical distribution is assumed; the distribution of seeds might be patchy in space and time, for example. The mechanism for hyperdispersal (B) might be different from (A), for example, dispersal by a different species of bird that rarely carries seeds, but does fly long distances. In the case of wind-dispersed species, Model A would involve the winds and storms that occur in most years, whereas Model B would invoke unusual storms (e.g. tornados) that could carry seeds distances several orders of magnitude greater. The outlying populations established in Model B would serve as 'infection centres' for the surrounding landscape, and as a source for further long-distance-dispersal ahead of the species frontier.

In the real situation beech and hemlock were advancing into previously established forest, which is not shown in Fig. 18.3. Within a forest, competition with other species for light and nutrients usually lessens the chances for successful establishment, and lengthens the time before first

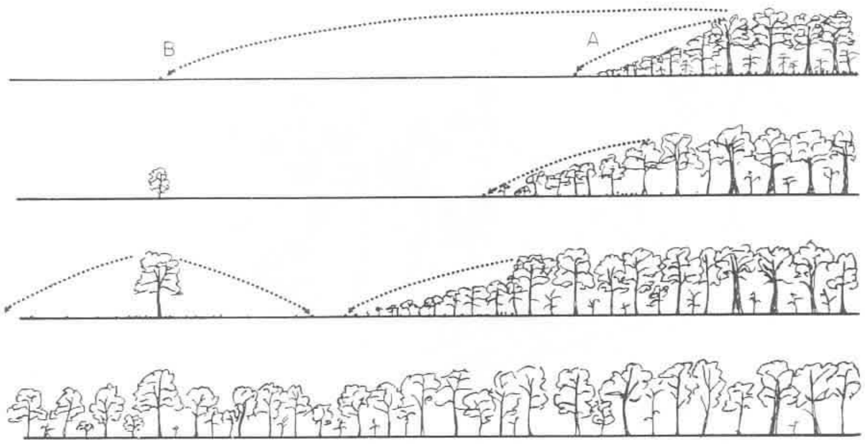

FIG. 18.3. Sketch of range extension for a hypothetical tree species: (A) advance as a continuous front; (B) advance as discontinuous populations, founded by long-distance dispersal of seeds. The vegetation that is being invaded is not shown in the sketch.

fruiting, thus slowing the rate of population growth. Slower population growth will affect the rate of advance of the species front and reduce the speed with which outliers act as 'centres of infection' expanding to form a continuous population over the entire landscape.

NATURE OF THE INVADING SPECIES FRONT

In order to consider beech and hemlock invasions using the diffusion models as a focus for discussion, we need to determine whether the species fronts were continuous or discontinuous. Pollen data from Davis *et al.* (1986) have been assembled from sites in sectors that include the longest radius of diffusion in the upper Great Lakes region. Different sectors were used for hemlock and beech (Fig. 18.4). Hemlock and beech pollen percentages at 1000-year intervals (from Davis *et al.* 1986) were plotted against the distances of the sites from the species front 150 years ago. Pollen percentages 150 years ago, from a somewhat larger data set including sites far outside the species limit (M.B. Davis, M.W. Schwartz & K.D. Woods, unpubl.), are also shown in Figs 18.5 and 18.7 for comparison.

Hemlock diffusion along an E–W transect across Upper Michigan and northern Wisconsin

Seven thousand years ago hemlock pollen appeared in trace quantities at a number of sites, and a significant percentage (>1·0%) appeared at one

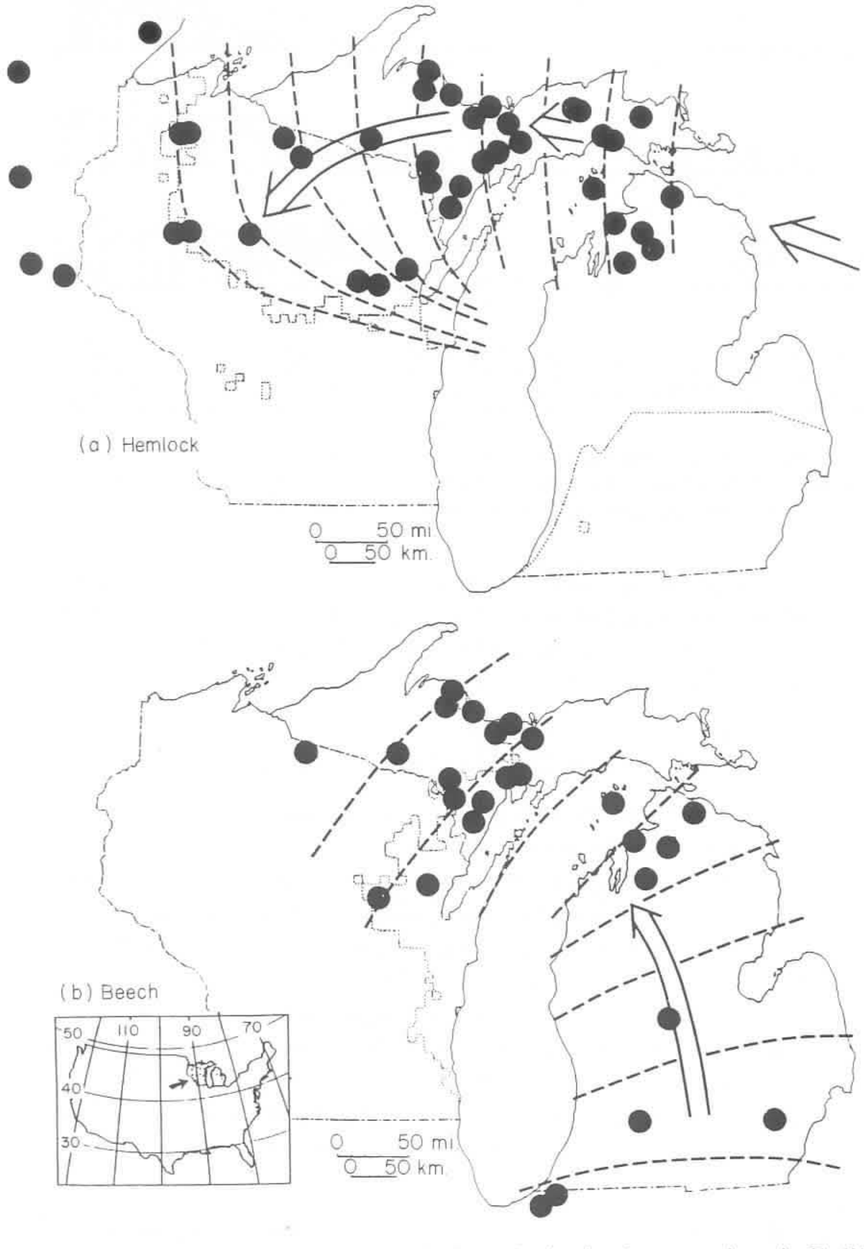

FIG. 18.4. (a) Outline map of Michigan and Wisconsin showing the sector along the E–W radius of diffusion of hemlock that was used for the tabulation of pollen percentages through time. Black dots indicate sites from which pollen data were summarized. (b) SE–NW radius of diffusion for beech. Black dots indicate the sites that were used for beech. Minnesota sites in (a) are from Birks (1976), Fries (1962), Waddington (1969), Wright & Watts (1969) and Wright, Winter & Patten (1963).

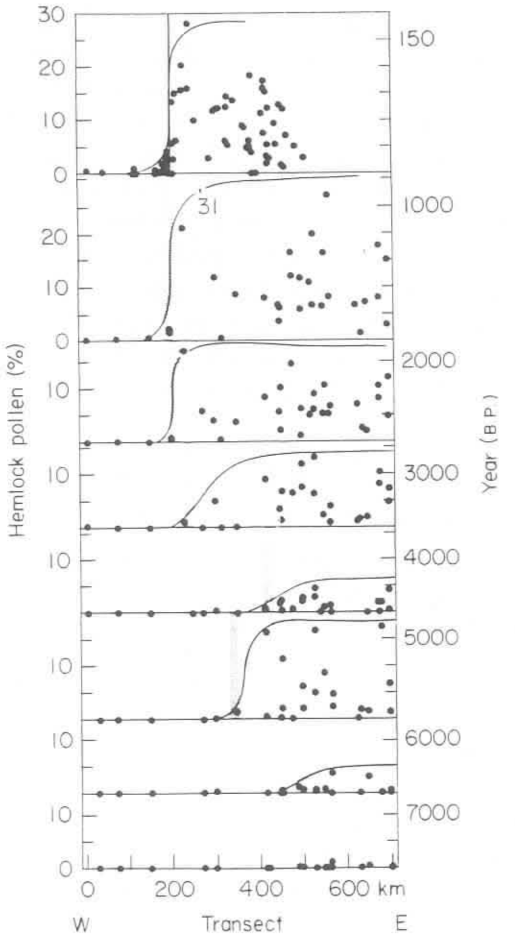

FIG. 18.5. Percentages of fossil hemlock pollen at 1000-year intervals from the series of small lakes across Upper Michigan and northern Wisconsin shown in Fig. 18.4a. Pollen percentages are plotted against distances from the species boundary 150 years ago. Data are from authors cited in legend for Fig. 18.1 and from Davis *et al.* (1986). Shaded lines indicate the probable positions of the species limit in the past.

site in Upper Michigan. Zero values characterized the western two-thirds of the transect (Fig. 18.5). Similar evidence from Lower Michigan suggests that isolated colonies may have become established before 6000 years BP in both Upper and Lower Michigan—a discontinuous front. During the next millennium, populations grew and coalesced, and a more or less continuous population was formed in the eastern part of Upper Michigan. By 5000 years ago a dense population had become established over an expanded arc with a steep species front resembling the hemlock front 150 years ago. Hemlock populations had spread rapidly, diffusing over an area larger than 50 000 km^2 in less than 2000 years.

During the next 2000 years hemlock populations declined steeply everywhere in eastern North America. A number of different lines of argument suggest that the decline resulted from the spread of a pathogen similar to the chestnut blight (Davis 1981b; 1983; Webb 1982; Allison, Moeller & Davis 1986). Along our transect pollen percentages declined, and there was an apparent retreat of the species front. By 3000 years BP populations had recovered and western advance resumed. The species front advanced about 50 km between 3000 and 2000 years BP, and about 25 km during the next millennium. We have not detected movement of the species front in Wisconsin during the last 1000 years.

Discussion of hemlock diffusion

The discontinuous model of diffusion describes hemlock during the first stages of invasion 6000 years ago. Apparently long-distance dispersal brought seeds 100–150 km from hemlock populations in Ontario. These early colonies acted as centres of infection for the remainder of the region, which was colonized quickly. Seed dispersal and the intrinsic rate of increase could have limited the spread of these rapidly expanding populations. Colonization occurred at about the same time in Upper and Lower Michigan, suggesting that Lake Michigan did not pose a significant barrier.

The initial colonization of Michigan through long-distance dispersal is not difficult to visualize for hemlock. Hemlock produces numerous small, winged seeds, which are shed throughout the autumn and winter months. They land on the surface of the snow and might easily be blown across the frozen surface of a lake, even a lake as large as Lake Michigan, the northern part of which freezes in winter.

Effective seed dispersal explains the large number of outlying populations to the west of the geographical range of hemlock (Fowells 1965). Prior to logging there were thirteen such populations in Minnesota, the farthest 150 km beyond the species limit (Fig. 18.6). The fossil record shows clearly that continuous populations of hemlock reached their present limit in Wisconsin 1800 years ago, with the subsequent establishment of a large outlier 20 km west of the limit 1300 years ago (Davis *et al.* 1986; unpublished data). The smaller outliers still farther west, in Minnesota, are not relict stands left from a previous continuous range, but new populations established by long-distance dispersal of seeds. Although prevailing winds blow from the west to the east, there are occasional

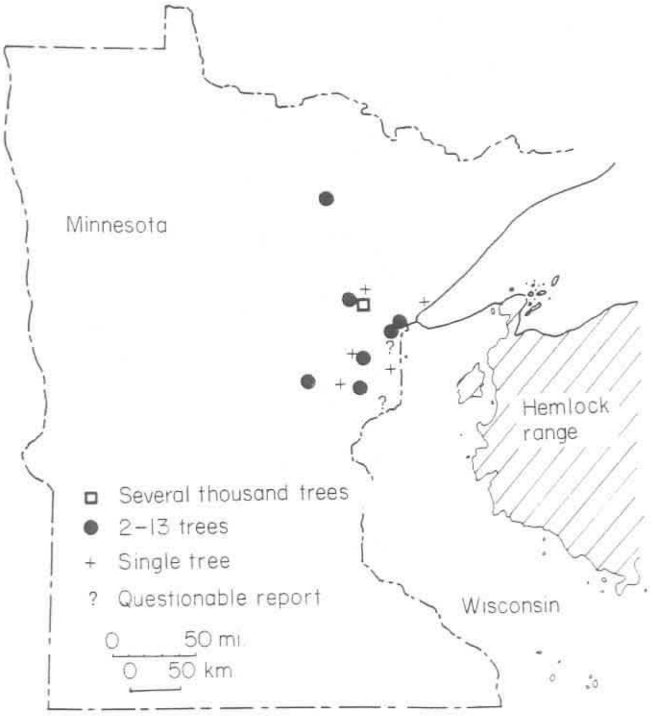

FIG. 18.6. Map of the distribution of hemlock in Minnesota and western Wisconsin in the early nineteenth century. Wisconsin occurrences are from the Land Office Survey Notes. The Minnesota occurrences were compiled from the records of the Heritage Program of the Minnesota Department of Natural Resources. Figure from Calcote (unpubl.).

storm winds in the opposite direction. These are apparently frequent enough to carry seed that becomes established in pockets of favourable habitat. The age of outliers to the south in Ohio and Indiana is not known, however. Some of these isolated populations could be relicts from a previously more extensive range.

Hemlock spread rapidly through eastern Michigan 6000–5000 years BP. Between 5000 and 1000 years BP, range extension occurred so slowly that seed dispersal can hardly have been a limiting factor. Problems in establishment, and slow population growth, apparently prevented hemlock from extending its range more rapidly. Once established, hemlock competes strongly with other plants because it casts a very dense shade. Young hemlock are more shade-tolerant than other species and can live for as long as 200 years before reproduction beneath a forest canopy.

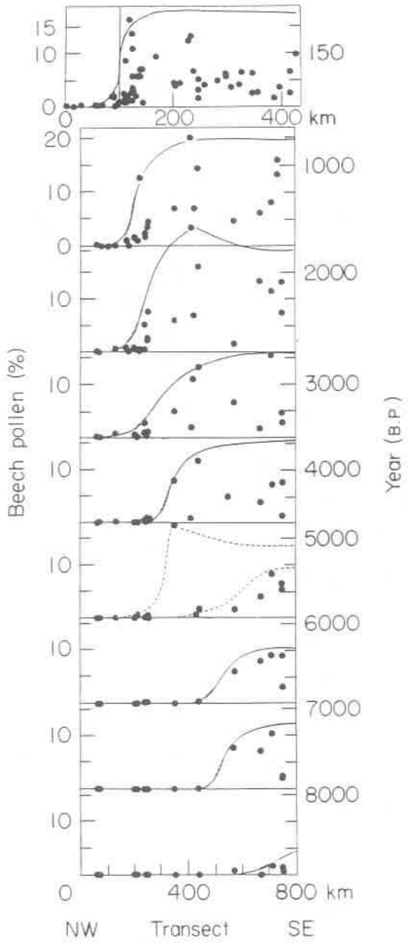

FIG. 18.7. Percentages of fossil beech pollen at 1000-year intervals from the series of small lakes shown in Fig. 18.4b. Pollen percentages are plotted against the distance of the site from the species boundary 150 years ago. Data are from authors cited in legend for Fig. 18.1 and from Davis *et al.* (1986). Shaded lines indicate probable locations of the species limit in the past.

Ring widths indicate that saplings can survive multiple episodes of suppression and release before reaching the canopy (Woods 1981). Once in the canopy, hemlock can live 600 or more years. Under these conditions age at first reproduction may be several centuries. As a result of the long generation length, the rate of population growth can be quite slow, and possibly limiting to the rate of spread.

Diffusion of beech along a SE–NW transect through Michigan and northern Wisconsin

Beech pollen percentages along the transect indicate that beech advanced northward through lower Michigan as a continuous population, reaching the straits that separate lower and upper Michigan by 5000 years BP. The total distance traversed was 400 km in 3000 years, an average rate of advance of 130 m per year. There was a general decline in percentages 5000 years ago; except for one tentatively dated site (Beaver Island: Kapp, Bushouse & Foster 1969) with very high percentages, the data from 5000 years BP fail to provide evidence for a steep front. The pollen percentages from 4000 years BP, however, indicate high abundances close to the species front. At this time an outlying population became established west of Green Bay on the far side of Lake Michigan. The newly established front on the west side of the lake was nearly stable for the next 1000 years. Between 3000 and 2000 years BP it advanced westward a few km, but there was extensive invasion of new territory in a direction perpendicular to the diffusion radius we are considering here (K.D Woods & M.B. Davis, unpubl.). The frontier moved westward slowly 2000–1000 years BP, advancing more rapidly between 1000 years BP and the present. During the last 4000 years, the rate of advance of the species front to the west has varied from 10 to 50 m per year, but there has always been some invasion of new territory.

Discussion of beech diffusion

Beech advanced along the diffusion radius as a continuous front. The only exception occurred as beech dispersed across Lake Michigan, establishing an outlying population on the western shore.

Beech nuts are dispersed by birds and mammals. Blue jays (*Cyanocitta cristata*) commonly feed on beech mast, which they cache near their nesting sites. The caches are placed just below the leaf litter layer on the forest floor, a site favourable for germination (Johnson & Adkisson 1985). Groups of about a dozen crowded beech seedlings germinating in the spring are not an uncommon sight, suggesting that birds often forget the locations of caches. The tendency of the birds to nest in woodland assures the placement of many cached nuts in habitats that are suitable for beech trees. Direct observations of jays in southern Wisconsin indicated that they transported beech nuts up to 4 km, making several 8 km round-trips each day (Johnson & Adkisson 1985). Dispersal by jays seems adequate for the advance of a continuous front at the rates we are reporting here, at least since 4000 years BP. Blue jays are probably adequate to explain the more rapid rates 8000–5000 years BP through Lower Michigan, although one is forced to assume a dispersal distance of 13 km and a generation length of 100 years, or dispersal 6–7 km and a generation length of 50 years, to explain the rate of advance. Although beech can fruit at 50 years when growing in an open situation (Fowells 1965), such short generations seem unlikely in a forest. A different means of dispersal might be necessary, however, to explain dispersal across open water. S.L. Webb (1986) suggests that the extinct passenger pigeon, a strong flyer that fed extensively on beech mast, could have been the agent for occasional long-distance dispersal events.

Beech is a strong competitor in northern hardwoods forests. It can persist in deep shade, growing slowly upwards toward the canopy. Saplings can often take advantage of small canopy gaps through rapid horizontal growth, outcompeting hemlock and sugar maple (*Acer saccharum*) (Thomas L. Poulson, University of Illinois-Chicago, pers. comm). Thus, it can persist and compete effectively for light gaps. In the absence of herbivores the survivorship of seedlings and saplings may be lower than hemlock, however, as beech cannot tolerate suppression by shade for as many years as hemlock (Woods 1981). It is difficult to assess seed production in beech near its western limit because it varies from year to year. 1984 was a good seed year in northern Michigan and beech populations were strongly represented by seedlings on the forest floor in the spring of 1985, indicating that reproduction by seed as well as by sprouting (Ward 1961) can occur near the western limit for the species.

INVASION OF FOREST COMMUNITIES

The pollen record from the northern Great Lakes region indicates that hemlock and beech were advancing into a forest mosaic where sugar maple and basswood (*Tilia americana*), and possibly yellow birch (*Betula lutea*) grew on wetter sites, and white pine (*Pinus strobus*), oak (*Quercus borealis*) and paper birch (*B. papyrifera*) grew on drier sites. During the last 3000 years, extension of beech and hemlock ranges was accompanied by a general expansion of mesic trees and a decrease of pine and oak. The changes suggest that a more moist climate permitted hardwood populations to expand, replacing pine, oak and paper birch on marginal sites (Davis *et al.* 1986; K.D. Woods & M.B. Davis, unpubl.). Although our data show regional invasion, they lack resolution to demonstrate changes within local communities. We do not know whether beech and/or hemlock moved first into newly established hardwood communities, participating in the displacement of pine, oak and paper birch, a successional sequence that can be observed today (T.L. Poulson, pers. comm.), or whether they immediately invaded old, established hardwood communities, where it was necessary to compete with longer-lived, shade-tolerant species such as sugar maple, basswood and yellow birch. Eventually they invaded these communities, as both beech and hemlock came to grow most abundantly on mesic sites. More detailed study utilizing small hollows that collect very local pollen could answer this question (M.W. Schwartz, unpubl.).

Because beech and hemlock seeds can tolerate dense shade, it seems reasonable that if their seeds were once dispersed into a forest, seedlings could become established and compete successfully with resident maple, basswood and yellow birch. The age-structure of beech in Dukes Experimental Forest, Michigan, suggests that this process may be occurring. The geographical limit of continuous beech populations occurs within an old-growth forest at Dukes that has been set aside as a scientific and natural area. Beech saplings can be found several tens of metres west of mature beech trees. Of course one has to make assumptions about the survival of the saplings to predict movement of the species frontier (Frederick Metzger, US Forest Service, pers. comm.). Similar observations are not available for hemlock, however. Hemlock seedlings are rare in most hemlock-hardwood forests, whether hemlock is dominant, or other hardwoods such as beech, sugar maple, basswood, or yellow birch are dominant. In these forests hemlock seedlings are established only in particular microsites, such as stumps or rotting logs (Curtis 1959). Because hemlock seedlings are preferentially browsed by deer in winter, mortality is high. Natural mortality rates are difficult to judge, however, because deer populations have been fluctuating due to human impact (Anderson & Loucks 1979).

Disturbance

Walker (1982) has suggested that periodic disturbance could have facilitated rapid range extension by opening communities to invasion. This may have been the case for beech in Europe, where the entry of beech into deciduous forests occurred at a time of intense prehistoric human disturbance (Iversen 1973). In North America, in contrast, recent human disturbance in the form of logging has caused a decrease in the abundance of both hemlock and beech. The change in hemlock density in Wisconsin is obvious in comparisons of maps prepared from Land Office Survey Notes (mid-nineteenth century) and maps of the present-day forest

(Davis, Schwartz & Woods, unpubl.). Pollen records in Wisconsin and New England also show decreased abundances of both species (Schwartz 1985; Davis 1985). Beech and hemlock appear to respond rather differently to natural disturbances, such as windthrow (Henry & Swan 1974). Furthermore, different kinds and frequencies of disturbances have different effects. The concept that disturbance promotes the entry of species into forest communities deserves discussion.

Frequency of disturbance

Frequent severe windstorms are a feature of the regional climate of north-central and north-eastern United States. The frequency of catastrophic windthrow of forest trees has been estimated from historical evidence such as maps of storm-damaged forests by nineteenth century Land Office surveyors, or from evidence within individual forest stands, such as fire scars on trees, tip-up mounds on the forest floor, or tree-ring sequences showing episodes of suppression and release (Lorimer 1985). Raup (1957), Stephens (1956), Lorimer (1977) and Schoonmaker & Foster (1985) all emphasize the importance of catastrophic windthrow damage to forests in New England. Lorimer (1977) used Land Office records to calculate the return time of large-scale catastrophic storms in Maine at 1150 years.

Lorimer recognized that vulnerable areas may experience severe storms frequently, while other sites may escape damage for longer periods than the regional average. In addition, frequency and intensity of storms varies from one geographical region to another. In central Massachusetts, tip-up mounds in a 0·25 ha forest plot were dated by ring-counts of trees growing on their surfaces. The age-classes of mounds suggested that strong winds had uprooted the larger trees in the forest approximately once per century for the last 450 years (Stephens 1956). Stephens was able to correlate three out of four episodes of windthrow with historical references to New England hurricanes in 1938, 1815, and 1635. An additional series of mounds were formed in 1850. The important point here is that hurricanes need not strike full force in a region, causing catastrophic damage, to have significant impact on the age structure of a forest community. Canham & Loucks (1984) make the same point.

In the northern Great Lakes region, tornados and violent downbursts of wind accompanying thunderstorms are major sources of disturbance. Tornados cause almost complete destruction to forest vegetation along a narrow path, twisting trees off at the base of the trunk. Downbursts affect larger areas, ranging from a few to 3800 ha (Stearns 1949; Canham &

Loucks 1984). Canham and Loucks calculate return times for catastrophic windstorms in northern Wisconsin at 1210 years. In southern Wisconsin downbursts are less common, but tornados, ice storms and fires occur at greater frequency (Canham & Louck 1984). The now extinct passenger pigeon was an additional source of disturbance, as forests (mainly oak or beech) used by nesting colonies were described as resembling sites of tornado damage (Bishop 1932). Roosts covered several km^2 and involved tens of millions of birds. The birds congregated so densely that branches were broken from trees, and droppings accumulated to a depth of several cm (Blockstein & Tordoff 1985; McKinley 1960). The return time is difficult to estimate, as the only records date from a period when the pigeon population was already in decline. Fire was the most important periodic disturbance along the prairie border (Grimm 1983), and to the north in the boreal forest, where the return time of fire averaged 100 years (Heinselman 1973).

Raup (1957) maintained that few if any American old-growth forests were all-aged, as might be expected if senescent trees were replaced one by one under equilibrium conditions. He argued that all stands that had been studied showed the effects of periodic disturbance: they were composed of cohorts, each of which originated following a disturbance that removed most of the canopy trees, permitting a new cohort of trees to grow to maturity. The age structure of a Wisconsin forest provides an example (Stearns 1949).

Disturbance and invasibility

Certainly the destruction of canopy trees helps invading species that are already present to grow rapidly to canopy size and thus to gain dominance more quickly (Davis & Botkin 1985). By increasing the light on the forest floor, or by increasing the frequency of gaps, disturbance might increase the growth rates of juvenile beech and hemlock, hastening maturation and fruiting. This mechanism would be effective in shortening the generation time for beech: maturation in just 50 years would have allowed diffusion of beech through lower Michigan at 130 m per year even if dispersal distance per generation were only 6–7 km. With a shortened generation time, the observed distances of seed dispersal by blue jays become sufficient to explain the rapid migration rates.

Entry to a forest community, however, is not necessarily facilitated by disturbance. Cut-over forests in the Great Lakes region often grow up into a dense stand of sugar maple saplings, or sugar maple and basswood sprouts. These successional stands cast dense shade and compete strongly for water and nutrients. They contain fewer young seedlings than mature forests (Bray 1956). The young, even-aged forest has fewer gaps than an all-aged stand, and thus fewer opportunities for rapid growth of invading seedlings. Invasion might succeed only if seeds arrived within the first year or two following disturbance, but even then beech and hemlock might be out-competed because their vertical growth rates in light gaps are slower than maple (Thomas L. Poulson, pers. comm.). In any case the probability seems small that a long-distance dispersal event would coincide in both space and time with a disturbance event.

Insight into the relationship between disturbance and invasion is provided by the Flambeau forest, an old-growth hemlock-hardwood stand west of the beach limit in Wisconsin that was flattened by a downburst storm in 1978 (Canham & Loucks 1984). Sprouts and seedlings of sugar maple and basswood are growing rapidly 7 years after the disturbance. Hemlock reproduction is poor, however (F.S. Stearns, University of Wisconsin-Milwaukee, pers. comm.). There were few hemlock seedlings in the stand prior to 1978, although hemlock was the dominant tree. Mature trees, which could have provided a seed source, were killed by the storm which occurred in July, before seed was mature. Of course there is no seed-bank in the soil for hemlock.

There is evidence, however, that hemlock establishment *can* be increased by certain kinds of disturbance. A small (0·4 ha) forest plot in southern New Hampshire was studied intensively by Henry & Swan (1974). The forest had originated following a windstorm and fire in the mid-seventeenth century. The ages of trees still living in 1967 show that beech recruitment is not correlated with disturbance: twenty-five beech trees have entered the stand since 1810, at the rate of about one per decade. The oldest hemlock trees entered the stand following a fire in the mid-seventeenth century. Several hemlocks were established in the centuries following, at apparently random intervals. The majority, however, became established during the past 150 years, just before or immediately following a series of windstorms which occurred in the early decades of the twentieth century. In this New Hampshire forest, the removal of canopy trees facilitated the growth and survival of previously suppressed hemlock in the understorey; frequent windstorms had the important effect of increasing the numbers of hemlock canopy trees (Henry & Swan 1974; Schoonmaker & Foster 1985; Lorimer 1985).

A similar response to windstorms has not been demonstrated in Michigan or Wisconsin. The disturbance regimes are different from New England, and frequently involve fire. It seems likely that forest succession following windstorm *and* fire is different from succession following windthrow alone. Intense fire sweeping through an area of blowdown would kill many of the hardwoods capable of sprouting, such as maple, basswood and beech. The seed bank in the soil would be destroyed, changing the competitive environment for invading species. In the Great Lakes region, reduction of the humus layer might provide a more favourable seedbed for hemlock. Experimental studies are needed to test these predictions.

A greater understanding of the processes of secondary succession in forests is essential to judge the chances of invasion through establishment following disturbance. Many studies of forest community structure emphasize gap-phase replacement in all-aged stands, compensatory recruitment, and the maintainance of diversity under equilibrium conditions. Succession following catastrophic disturbance deserves the greater emphasis that it is receiving in the most recent literature (Pickett & White 1985).

CONCLUSIONS

Fossil tree pollen in sediments records rapid range extensions, demonstrating that temperate forest communities of North America and Europe have been invaded repeatedly by forest species during the last 10 000 years. The rates at which species have been able to extend their ranges, and by inference to invade forest communities, have varied over space and time. In this chapter I have discussed some of the factors that could have limited range extensions of two species, beech and hemlock. At this point the most rapid rates recorded by fossil pollen can be explained by processes that have been observed in modern forests, such as dispersal of beech nuts by jays. The occurrence of outlying populations west of the hemlock range makes it clear that probabilities are relatively high for long-distance dispersal in this species, explaining hemlock's rapid invasion of Michigan between 6000 and 5000 years BP. Seed dispersal, even for trees that characterize old-growth forest, is surprisingly effective. Therefore, it seems likely that during most of the history of the invasion of the Great Lakes region, invasion occurred more slowly than if it were limited by seed dispersal *per se*.

Variables such as seed production, seedling establishment, seedling and sapling mortality, and generation length were far more important. The ways in which these parameters are influenced by climate must be understood before the fossil record of past changes in geographical distribution can be accurately interpreted as a record of climate. Much can be learned about the influence of community context on these parameters by studying secondary succession in forests, especially the succession that occurs in forest undisturbed by human activities following episodes of natural disturbance. Information about the establishment of seedlings, and the outcome of competition as forest stands mature and humus layers accumulate, is needed to understand the evidence contained in the fossil record regarding the rates at which forest communities were invaded by beech and hemlock.

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